

WHITE SPRUCE MEETS BLACK SPRUCE: DISPERSAL, POSTFIRE ESTABLISHMENT, AND GROWTH IN A WARMING CLIMATE

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Abstract. Local distributions of black spruce (*Picea mariana*) and white spruce (*Picea glauca*) are largely determined by edaphic and topographic factors in the interior of Alaska, with black spruce dominant on moist permafrost sites and white spruce dominant on drier upland sites. Given the recent evidence for climate warming and permafrost degradation, the distribution of white spruce is expected to expand, but the transition from black to white spruce may be dispersal limited: unlike the semi-serotinous black spruce, postfire regeneration of white spruce relies on seed dispersal from unburned areas. To determine the relative roles of dispersal, establishment, and growth in recruitment of white and black spruce, we studied postfire spruce regeneration in a 21-year-old burn across a white spruce-black spruce transition in the interior of Alaska. Although prefire spatial distributions of adults of the two species were well separated along the topographic sequence from upland to floodplain sites, the spatial distributions of recruits overlapped considerably. Even >700 m away from its seed source, white spruce sapling density on typical black spruce sites was high enough to form fully stocked stands. In contrast, black spruce regeneration was sparse on typical white spruce upland sites. Establishment rates of both species, estimated from a statistical model, were highest in mossy, wet depressions, which tended to have a thick residual postfire organic layer (~10 cm). On all site types, height growth rates inferred from age-height relationships were comparable for recruits of both species. On typical black spruce sites >300 m into the burn, white spruce was younger (and, therefore, shorter) than black spruce due to the timing of masting events following the fire. There was no indication that dispersal, establishment, or edaphic constraints on juvenile growth limit white spruce's capacity to invade typical black spruce stands during the recruitment stage in our study area. It is unlikely that white spruce recruits would persist to the adult stage if the permafrost returned to the original prefire levels during future postfire succession. However, if permafrost continues to degrade under climate warming, transition to a white spruce-dominated landscape could be rapid.

Key words: Bayesian analysis; black spruce; detrended correspondence analysis; fire severity; long-distance dispersal; negative binomial; organic layer; permafrost; recruitment; spruce seedling identification; survival; white spruce.

INTRODUCTION

Vegetation shifts induced by global warming have been identified as important feedbacks affecting climate change (Chapin et al. 2005, McGuire et al. 2006). Black spruce (*Picea mariana* [P. Mill.] B.S.P.) and white spruce (*Picea glauca* [Moench] Voss) are the two main forest-forming tree species in the interior of Alaska, each comprising ~40% of the total forest area (Yarie and Billings 2002). The contemporary distribution and habitat associations of black and white spruce forests are well documented (Yarie 1981, Viereck et al. 1983, Chapin 1986, Dyrness et al. 1989, Chapin et al. 2006). Black spruce typically occupies poorly drained lowlands and north-facing slopes, where permafrost restricts

drainage, whereas white spruce often dominates well-drained floodplains and warm upland soils that lack permafrost.

Climate and edaphic conditions in the interior of Alaska are changing rapidly. The growing-season temperature in the last 30 years has increased by 0.4°C per decade (Chapin et al. 2005), permafrost is warming and decreasing in areal extent (Osterkamp and Romanovsky 1999), and lakes are shrinking in regions of discontinuous permafrost, which suggests altered drainage patterns due to permafrost degradation (Smith et al. 2004, Riordan et al. 2006). In addition, the annual area and severity of fires has increased in recent decades (Kasischke et al. 2006), which may further accelerate the thawing of permafrost if insulating moss and soil organic layers are consumed by fire. A retreat of permafrost should generally favor white over black spruce, but model predictions of vegetation response to changes in climate and fire regime (e.g., Rupp et al.

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2002) are difficult to validate because little is known about the relative importance of different recruitment processes (e.g., seed dispersal, establishment, and growth) across environmental gradients.

Under boreal conditions, species turnover in mature forests is typically slow, and gap phase dynamics play a subordinate role. This compositional inertia is broken by fire, and different endpoints may be reached in the subsequent secondary succession, depending upon the environmental conditions during the early postfire stage and a number of contingent factors (fire severity, timing of mast years, etc.; Johnstone and Chapin 2003, Peters et al. 2005). As the annual area burned grows and the climate becomes warmer and drier, an increasing proportion of the landscape is disposed to undergo changes in vegetation composition.

Postfire recruitment can be partitioned into three major processes: (1) seed dispersal, (2) establishment (i.e., germination and seedling survival), and (3) post-establishment performance. The first two steps occur during the first 5–10 years after the fire and determine the initial relative abundances of species. Once established, spruce recruits in regenerating burns in the interior of Alaska tend to suffer little mortality (Johnstone et al. 2004, Johnstone and Chapin 2006b); thus, postestablishment attainment of dominance is primarily determined by growth performance in this system. The above three steps are controlled by different factors. Seed deposition decreases with distance from seed source for white spruce and increases with prefire basal area for the semiserotinous black spruce, which forms a canopy seed bank (Dobbs 1976, Zasada 1986, Greene et al. 1999, Greene and Johnson 2000). Germination and seedling survival of both spruce species during the early sensitive stage strongly depend upon the moisture status of the topsoil (which itself depends upon climate, microtopography, and organic-layer thickness) and competition with grasses (Cater and Chapin 2000, Johnstone and Chapin 2006a). Conditions beneficial for establishment may differ from those required for high growth rates. Growth rates of recruits and also adults depend most strongly on active layer thickness (depth of nonfrozen soil), soil temperature, and nutrient supply (Dyrness et al. 1989).

Because the seedling and sapling stages of recruitment are directly or indirectly affected by climate, they are sensitive to climate warming. A warmer, drier climate may reduce initial establishment but lead to increased growth rates thereafter, especially in white spruce, which grows more rapidly and is more responsive to nutrients than black spruce (Chapin 1986). Climate envelope models of vegetation distribution ignore dispersal limitation and assume that propagules of all species are omnipresent in the landscape (Prentice et al. 1992, Tchepakova et al. 1993). Under this assumption, vegetation boundaries respond rapidly to climate change. However, if seeds do not reach sites that have become favorable for growth under a changing climate,

recruitment will be limited by dispersal, and vegetation boundaries will shift more slowly than predicted by climate envelope models.

We studied postfire recruitment of black and white spruce in a 21-year-old burn covering a white spruce–black spruce transition along an upland–floodplain gradient in the interior of Alaska, USA. We quantified abundance and growth rates of recruits along transects that began at the edge of an unburned white spruce forest on warm upland soils and extended up to 800 m into an area underlain by permafrost that was dominated by black spruce prior to the fire. In this paper, we address the following questions related to the three recruitment stages (dispersal, establishment, and growth): (1) Are abundances of recruits of the two species well-separated along topographic/edaphic gradients, as are adult abundances? (2) If there is substantial overlap in recruit distributions, what are the likely explanations (long-distance dispersal, substrate preferences of recruits differing from those of adults)? (3) How do growth rates of recruits of the two species compare inside vs. outside their respective adult habitats?

METHODS

Study area

The study area was located in the interior of Alaska, 30 km southwest of Fairbanks, at the Bonanza Creek Long Term Ecological Research (LTER) site. This area includes water-logged black spruce forests in the Tanana River floodplain, productive upland white spruce forest, and self-replacing trembling aspen (*Populus tremuloides*; hereafter, "aspen") forests on dry south-facing slopes (Foote 1983, Viereck et al. 1983). Spruce recruitment was studied 21 years after the Rosie Creek burn. In late May 1983 this intense fire burned 3480 ha of forest both in the floodplain and upland areas. Apparently, all trees were killed within the burned area (Juday and Dyrness 1985, Densmore et al. 1999; LTER site descriptions, G. P. Juday, *personal communication*). The fire left an unburned "peninsula" of mature, mixed, white spruce–hardwood forest that now protrudes on a ridge into the burned matrix (Fig. 1). This stand was the primary seed source for postfire white spruce recruitment in the burned area. Its basal area is comprised of paper birch (*Betula papyrifera*; 20.5 ± 11.0 [mean $\pm$ SD] m^2/ha), aspen (8.3 ± 7.3 m^2/ha), and white spruce (11.4 ± 5.7 m^2/ha), with white spruce reaching a height of ~ 25 m (maximum, 36 m) and exceeding the hardwoods in height by ~ 5 m. Stem densities of the three species were 92 ± 88 , 608 ± 188 , and 333 ± 58 trees/ha, respectively (trees with diameter at breast height [dbh, measured at 1.3 m above the ground surface] > 10 cm). The stand has an organic-layer thickness of 11.6 ± 1.5 cm and an east-facing slope of $9.7^\circ \pm 4.1^\circ$. The typical prefire black spruce stand in the floodplains was monotypic, had a stand age of 65 yr, a basal area of 7.2 ± 5.4 m^2/ha , a stem density of 18000 ± 12600 trees/ha, and a mean tree height of 2–3 m (maximum 6 m).

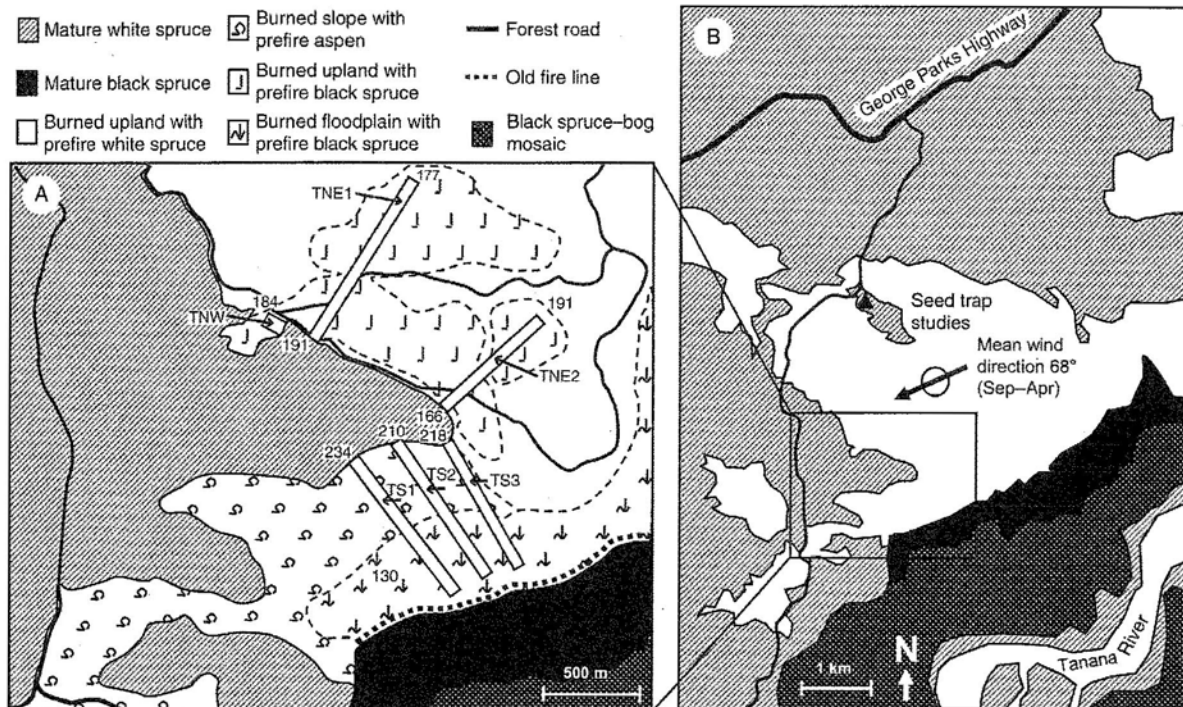


FIG. 1. (A) Study area within the (B) Bonanza Creek Long Term Ecological Research (LTER) site, Alaska, USA. (A) Three southern (TS1, TS2, TS3) and three northern (TNW, TNE1, TNE2) transects extended from the unburned white spruce forest "peninsula" into the surrounding 1983 Rosie Creek burn. The burned area could be roughly divided into three regions: (1) a south-facing slope with abundant postfire aspen regeneration; prefire stand primarily aspen and white spruce with admixture of black spruce toward the lower slope; (2) flat upland with frequent permafrost; postfire regeneration primarily spruce; prefire stand primarily black spruce with occasional birch; (3) floodplain with moss-dominated wet depressions; postfire regeneration primarily spruce; prefire stand of black spruce. The fire was stopped by a bulldozed fire line on the south border of the burned floodplain area. Numbers are elevations in meters. (B) Our transects were positioned in the southern part of the Rosie Creek burn (white area). Two seed trap studies were conducted around the northern white spruce forest "peninsula" by Zasada (1986) and Rupp (1998). The location of the climate station is indicated by a solid triangle.

Sampling design

In total, 99 plots were established along six transects around the southern unburned white spruce "peninsula." All transects started at the edge of the white spruce forest (which we assumed was the primary seed source for white spruce regeneration in the burn) and extended perpendicular to the forest edge into typical black spruce habitats within the burn. Three transects were oriented to the north and three to the south (Fig. 1A). Transects were arranged to sample different topographical aspects in order to obtain different combinations of edaphic conditions and distance to white spruce seed source. Along each transect, square plots were located at the following positions: 0 m (which was the plot starting directly at the source stand edge into the burned area), 10, 25, 50, 75, and 100 m, and then at 50-m increments up to 800 m. Distances used in the dispersal model are horizontally corrected and therefore deviate slightly from the above scheme. Some transects intersected forest roads or areas affected by salvage logging; in these cases, the above scheme was modified, with plots shifted along the transect in 25-m increments until there

was no longer any sign of human disturbance. The far ends of the three southern transects were highly variable with respect to edaphic conditions and prefire basal area of black spruce. To ensure that these predictors were not confounded with distance from the white spruce source stand, we stratified our sampling at positions 550 m and 725 m along southern transect 1 (TS1) and TS2 and at 450 and 650 m along TS3. At each of these positions, we randomly located three plots within each of three strata: (1) moss-dominated depressions with low prefire basal area of black spruce, (2) moss-dominated depressions with high prefire basal area of black spruce, and (3) elevated micro-ridges. These strata belong to the site types "Moss" (strata 1 and 2) and "Ledum" (stratum 3) defined below. Depending on our visual impression of recruitment density, plot sizes varied from 12 to 100 m², with larger plots used for areas with sparse recruitment.

We recorded the species identity and height of all spruce recruits within plots, where "recruits" refers to all individuals present at the time of sampling (2004; 21 years postfire). Although many individuals were <25 cm tall, age distributions suggest that >90% of recruits established within 10 years of the fire (see Results). Thus,

even small individuals were typically >10 yr old and had thus already survived the early sensitive stage. In total, 6244 individual spruce recruits were identified and measured. Source stand basal area composition was quantified in three 10×40 m plots inside the source stand positioned parallel to the forest edge near the initiation of transects TS1, TS3, and northeastern transect 1 (TNE 1).

Identification of black and white spruce recruits

Although white spruce and black spruce are easily distinguished as mature trees (Viereck and Little 1972), seedling and sapling identification has previously relied on features such as the hairiness and color of young twigs, color and sharpness of needles, and bark flakiness. All of these features are highly variable, especially in response to the light environment (V. Peters, *personal communication*). The presence of teeth along seedling needle margins, when present, is a reliable feature of white spruce (Viereck and Little 1972). In most cases, however, we relied on an identification method that we developed based on the arrangement of needle resin ducts (Weng and Jackson 2000; Appendix A), which allowed for reliable identification of nearly all individuals in the field.

Reconstruction of prefire stand composition and density

Prefire basal areas of black and white spruce were reconstructed by measuring diameter at breast height of all dead trees (snags and logs) in each plot, which ranged in size from 12 to 100 m^2 , depending on the size and density of prefire trees. In most cases, prefire basal area reconstruction was straightforward because live trees are rarely consumed in fires (Lorbert and Warnatz 1993), most ($>95\%$) dead trees showed little or no sign of decay above the root collar, and most individuals (78%) could be unambiguously identified to species based on cone features. Black spruce has small ovoid cones typically attached to short side branches close to the stem at the top of the crown forming a cone ball, whereas white spruce has more elongated and larger cones on unspecialized side branches. For the 22% of the individuals for which cones were not found, a logistic regression model was developed to predict species identity based on other morphological features (size, adventitious roots, ring width patterns; Appendix B). This model explained 69% of the deviance in the calibration data set.

Modeling dispersal and establishment

To study the relative roles of seed dispersal and establishment on recruitment, we developed statistical models for the abundance of black and white spruce recruits based on two groups of predictor variables: those related to seed rain (number of viable seeds arriving at a site) and those related to establishment rate (fraction of viable seeds that germinated and survived to 21 years postfire).

Seed rain predictor variables

For white spruce, we assumed that seed rain at each location in the burn was a function of the minimum distance to the source stand (which in 95 out of 99 plots was equal to the transect position) and seed production in the source stand, which we estimated from seed trap data (Appendix C). Although wind direction and velocity are potentially important factors influencing dispersal, we did not account for these factors in our model because wind data were not available for the relevant dispersal years and because we were concerned that an overly complex model would be poorly constrained by the modest number of plots in our data set. Nevertheless, to explore the potential influence of white spruce seed sources (other than the presumed source stand from which dispersal distances were calculated), we analyzed hourly wind data for the years 1998–2004 (Appendix D). The mean wind direction during the abscission period (September–April) was $68.2^\circ \pm 79.5^\circ$. For the majority of the plots the nearest forest edges in the direction of the prevailing northeasterly winds were >2 km from our transects (Fig. 1B) and were thus unlikely to contribute substantial seed rain.

In contrast to white spruce, most seeds of the semiserotinous black spruce disperse locally around the typically short-statured parent trees directly after fire. Therefore, for black spruce, we assumed that seed rain at each location in the burn depends on the local prefire basal area of black spruce (Greene et al. 1999).

Establishment predictor variables

Four variables, described in detail here, were used to model establishment rate: reconstructed organic-layer thickness that remained after the fire (olt_0), the percent cover of the competitive grass *Calamagrostis canadensis* (*g*), and the first two axis scores of a detrended correspondence analysis (DCA; Hill and Gauch 1980) of vegetation cover data (DCA1 and DCA2). The first two variables were selected based on a priori knowledge of their importance in spruce germination and survival (Zasada 1986), while the DCA scores were used as surrogates for environmental gradients (e.g., soil moisture and nutrient status). To aid in interpreting the DCA axes, we recorded several auxiliary environmental variables, but, to avoid problems arising from collinearity, we did not use these as predictors of establishment.

The organic soil horizon was examined in the field in five profiles per plot (one in the plot center and four closer to the plot corners), and plot means were recorded for the thicknesses of the total organic layer at 21 years postfire (Olt_{21}) and the residual organic layer present immediately following the fire (olt_0). The total organic layer (Olt_{21}) included olt_0 , dead organic material that had accumulated since the fire, and live moss. The border between the mineral soil and the organic horizon was identified from texture differences. The border between olt_0 and the new organic layer formed since the fire was,

in most cases, indicated by a charcoal horizon. In addition there were clear differences between these two layers in texture (olt₀, dense and sticking to fingers; new layer, soft and not sticking to fingers) and color (old, black with homogeneous appearance; new layer, brown and consisting of mostly undecomposed mosses).

The percent cover of all plants (62 species or species groups, respectively) was visually estimated. The cover of cryptogams (lichens and mosses), small species of higher plants, litter, and bare soil was estimated along three 1-m transects per plot. The DCA ordination of the cover data was implemented with PCORD (McCune and Mefford 1997). Species occurring in fewer than three plots were excluded from the analysis. Plot scores along the first two DCA axes were used as explanatory variables of establishment and to define site types, which were used as a categorical grouping variable in several figures and analyses. For more information on the vegetation survey see Appendix F.

The slope of each plot was measured with a clinometer, and the aspect was recorded if the slope exceeded 3°. The thickness of the active layer (i.e., the nonfrozen soil) was measured with a 130-cm permafrost probe between late July and early September (mean of five probes per plot). We made no attempt to measure permafrost below 130 cm.

Statistical modeling of recruitment functions

For each species, we assumed that the number of viable seeds arriving in plot *i* was a negative binomial random variable s_i with mean S_i and variance $\hat{s}_i + \hat{s}_i^2/r$ (r being the shape parameter of the negative binomial distribution), and that the number of recruits was a binomial random variable with s_i trials and probability of success (i.e., establishment) p_i . In Appendix E, we show that the above assumptions imply that the distribution of recruits in plot *i* is negative binomial with mean $\mu_i = \hat{s}_i \times p_i$ and variance $\mu_i + \mu_i^2/r$.

For each species, mean seed arrival, S_i , was calculated as the product of the area of plot *i* (in square meters) and mean viable seed rain at plot *i* (in numbers of seeds per square meter). For white spruce, mean viable seed rain was modelled with a function modified from Clark's 2Dt dispersal kernel (Clark et al. 1999):

$$\text{mean seed rain}_i = \frac{w_1}{(1 + d_i^2/w_2)^{w_3}}$$

where d_i is the distance from the edge of the source stand to plot *i*, w_1 is seed rain at the forest edge ($d = 0$ m), and w_2 and w_3 are scale and shape parameters, respectively. The shape of this function is flexible both near the origin and in the tail and has its highest value at zero distance, as expected for an area source. Black spruce mean seed rain was modeled as

$$\text{mean seed rain}_i = b_1 + b_2 \text{BA}_i$$

where BA_i is the reconstructed prefire black spruce basal area in plot *i*, and b_1 and $b_2 \text{BA}_i$ are global and local

components, respectively, of seed rain (Greene et al. 1999, 2004).

For each species, establishment probability (i.e., the number of recruits at plot *i* per arriving viable seed) was estimated with a logistic function,

$$p_i = e^{\theta_i} / (1 + e^{\theta_i}),$$

where θ_i is a linear combination of the establishment predictors

$$\begin{aligned} \theta_i = & \beta_0 + \beta_1 \text{olt}_{0i} + \beta_2 g_i + \beta_3 \text{DCA1}_i + \beta_4 \text{DCA2}_i \\ & + \beta_5 \text{DCA1}_i \text{olt}_{0i} + \beta_6 \text{DCA2}_i \text{olt}_{0i}. \end{aligned}$$

All establishment predictors were standardized to mean zero and unit variance, so the magnitudes of the β 's reflect the relative impact of each variable on establishment, the intercept β_0 is the estimated logit of the establishment probability when all covariates are at their mean value, and the main effect of each covariate appearing in an interaction term reflects its effect on establishment probability when its interacting "partner" is at its mean value. Interaction terms for g were not considered because it was highly correlated with the other covariates.

We performed Bayesian analyses using WinBUGS 1.4.1 (Spiegelhalter et al. 2002). For each model, three chains were run in parallel, and convergence of the posterior distribution for each parameter was assessed by convergence to one of the ratio of pooled to mean within-chain central 80% intervals and by stability of both intervals (Brooks and Gelman 1998). For each species, we began with a full model including all predictor variables. To obtain a parsimonious "best candidate" model, we sequentially eliminated variables whose 95% credible intervals included zero, rerunning the model after each elimination. These eliminations typically improved the model's predictive ability as measured by the deviance information criterion (DIC; Spiegelhalter et al. 2002). We also examined white spruce models in which the negative binomial shape parameter r varied with distance from the source stand, as well as black and white spruce models in which the distribution of recruits was assumed to be Poisson, rather than negative binomial. Finally, we ran the analysis with the northwestern transect (TNW) excluded, because the far end of this transect may have been influenced by additional seed sources to the northwest (Fig. 1). These modifications did not qualitatively affect our results and are not presented. Prior distributions were noninformative for all parameters except for w_1 (white spruce seed rain at distance zero from source stand), which was Gaussian with 207.9 ± 8.1 seeds/m² (mean $\pm$ SD; Appendix C).

Growth performance and height and age distributions

Height distributions were compared between species and the four site types. Comparisons of log-transformed heights were performed between species within a site type with two-tailed *t* tests and within species between site types with ANOVA followed by a post hoc test (1m and multicomp functions in S-Plus 6.1 [Insightful

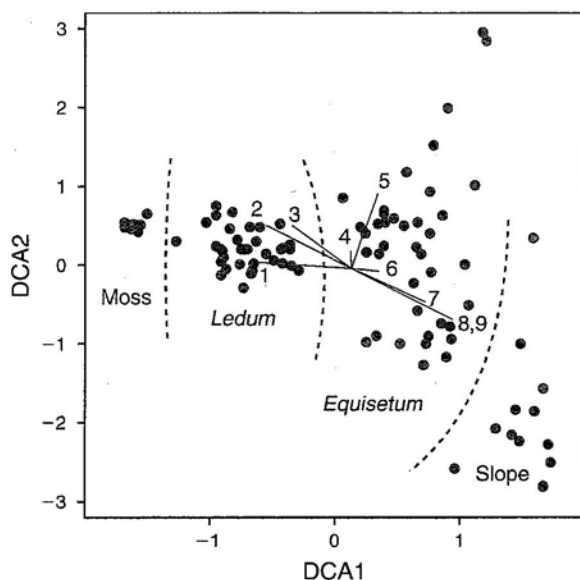


FIG. 2. Ordination of vegetation plots and correlations with environmental variables (line lengths are proportional to correlation strength). Detrended correspondence analysis (DCA) was used to calculate axis scores (DCA1 and DCA2), and scores were standardized to mean zero and unit variance. Each plot was assigned to one of four "site types," as indicated by the dashed lines. Environmental variables recorded for each plot are indicated by numbers and include total organic-layer thickness 21 years postfire (2), organic-layer thickness immediately after the 1983 fire (3), prefire black and white spruce densities (1 and 6, respectively), postfire basal area of aspen and birch regeneration (9 and 4, respectively), active-layer thickness (7), slope percentage (8), and cover of the grass *Calamagrostis canadensis* (5).

Corporation, Seattle, Washington, USA] using Tukey's method). Age-height curves were constructed to (1) compare growth performance of black and white spruce within different site types and (2) estimate age distributions from observed height distributions. The estimated age distribution for white spruce, in turn, was used to estimate the proportion of recruits originating from long-distance seed dispersal (>300 m), as opposed to recruits that might have originated from short-distance dispersal (300 m) within the burn (see *Discussion* for details). Within each of three site types (Moss, *Ledum*, and combined *Equisetum*/Slope; see *Results* for site type definitions), we aged 37–52 recruits per species outside the plot areas. Within each species, we sought to sample an approximately equal number of recruits in each of four height classes centered on 25, 50, 100, and 250 cm. In total, 305 recruits were aged. Because in most cases the stem position of the hypocotyl could not be clearly identified, recruits were excavated with their root stock. For each recruit, up to seven cross sections around the base of the stem were dated, and the age of the oldest cross section was taken as the recruit age. Details about the model-fitting procedure and error propagation for the height-age conversion are presented in Appendix G.

RESULTS

The DCA ordination revealed four distinct vegetation groups separating primarily along DCA1 (Fig. 2), which was positively correlated with slope (Pearson's $r = 0.66$), active layer thickness ($r = 0.56$), and basal area of aspen regeneration ($r = 0.57$) and negatively correlated with total organic layer thickness $0lt_{21}$ ($r = -0.61$; Table 1). Thus, DCA1 can be interpreted as a temperature-soil moisture gradient from cold and poorly drained depressions dominated by mosses such as *Aulacomnium palustre* (Moss site type) to warm and dry south-facing slopes characterized by *Shepherdia canadensis* and aspen regeneration (Slope site type; Appendix F). The intermediate classes consisted of a dwarf-shrub community dominated by *Ledum* spp. and *Vaccinium Vitis-idea* (*Ledum* site type) and a community of several species, dominated by *Equisetum pratense* (*Equisetum* site type), indicative of more basic soils (Foote 1983). Detrended correspondence analysis axis 2 was positively correlated with the cover of the grass *Calamagrostis canadensis*. The correlations of DCA2 with slope and $0lt_{21}$ were in opposite directions as compared with DCA1 and less pronounced ($r = -0.45$ and 0.42 , respectively).

There was considerable variation in sapling densities and environmental conditions across all transects (Fig. 3). Variability in site conditions was stronger and more directional along the southern transects than along the northern transects. The southern transects initially descended an aspen-dominated slope connecting the unburned white spruce forest on the ridge with the floodplain across an elevation gradient of 80 m. Depending on the microtopography, the site type along the southern transects' first 400 m was *Equisetum* or Slope (mean slope $13^\circ \pm 7^\circ$ and $24^\circ \pm 14^\circ$, respectively). In the floodplain, the site type changed abruptly to either *Ledum* or Moss, and permafrost (active layer depth < 130 cm) was common. In the northern transects the slope rarely exceeded 10° (Fig. 3C). The permafrost was patchy, and the site type alternated between *Ledum* and *Equisetum* (Fig. 3G). There were no dry sites (Slope site type) far from and no moist sites (Moss type) close to the white spruce forest edge on any transect (Appendix H). The postfire organic layer thickness alto

TABLE 1. Pearson correlations of environmental and vegetation variables with the first and second detrended correspondence analysis ordination axes (DCA1 and DCA2).

Variable	DCA1	DCA2
Active layer thickness (cm)	0.564	-0.379
Slope ($^\circ$)	0.659	-0.451
Total organic layer thickness (cm)	-0.611	0.416
Postfire basal area of birch (m^2/ha)	0.091	0.269
Postfire basal area of aspen (m^2/ha)	0.569	-0.381
<i>Calamagrostis canadensis</i> cover (%)	0.309	0.537

Note: The first DCA ordination axis, DCA1, can be interpreted as a moisture/temperature gradient ranging from cold, moss-dominated floodplain sites to warm, dry, slope sites.

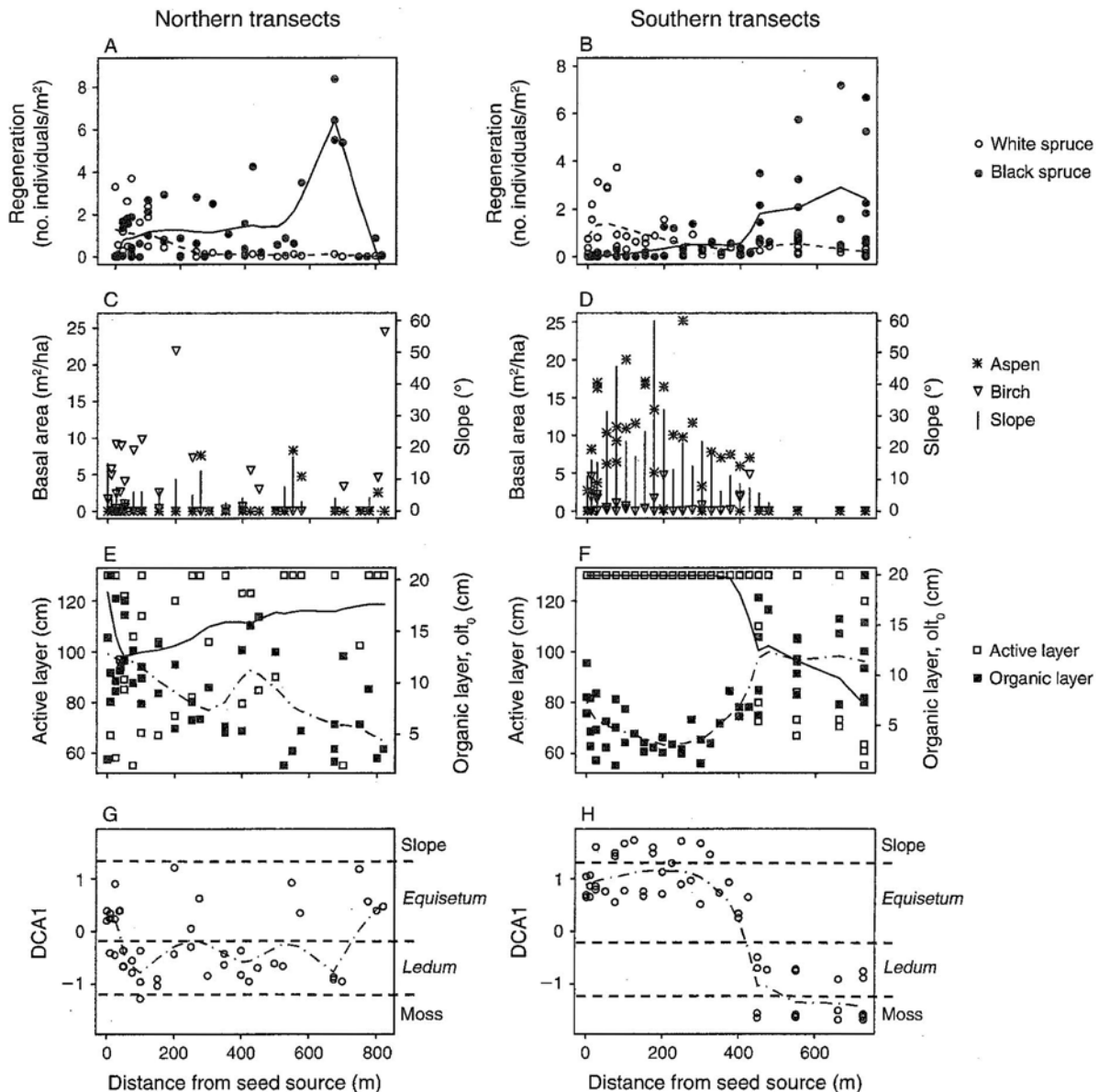


FIG. 3. Regeneration densities and environmental gradients along the northern and southern transects. Panels show (A, B) spruce regeneration densities, (C, D) basal area of co-occurring hardwoods, (E, F) active-layer and postfire organic-layer thickness, and (G, H) the vegetation/moisture gradient represented by detrended correspondence analysis axis 1 (DCA1) scores. Curves were fit to the data using a variable span smoother in S-Plus (Friedman 1984). In panels (G) and (H), the dashed lines separate the site types identified with DCA (Fig. 2).

was often higher close to the forest edge, most likely because of low fire severity near the edge of the burn.

Across all transects the density of white spruce recruits decreased with increasing distance from the forest edge (Fig. 3A, B), but the decline was less pronounced for the southern transects, where even at a distance of 725 m the mean density was still as high as 0.4 individuals/m². Black spruce densities were highest in the floodplain habitat in the southern transects (up to 7.5 individuals/m²). The peak in black spruce densities at

~700 m along the northern transects corresponded to a severely burned patch.

The deadwood analysis (prefire stand) supported the well-known association of white spruce with warm upland soils and black spruce with cool/moist soils (Fig. 4). Mature prefire individuals of white spruce were found in only five of 47 plots in the Moss and *Ledum* site types, but were abundant in the *Equisetum* and Slope site types. In contrast, mean prefire black spruce density was highest in the Moss and *Ledum* site types (up to 4.3

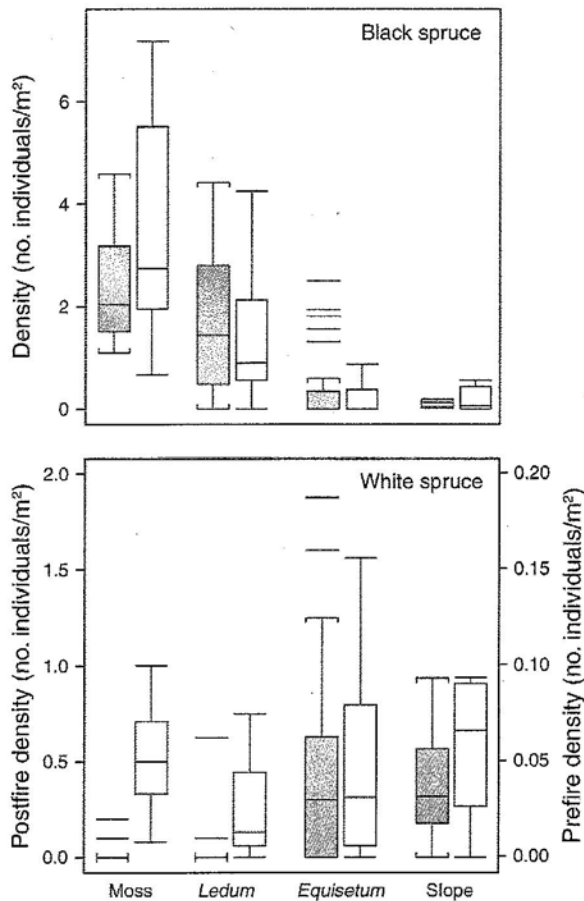


FIG. 4. Density of recruits (white boxes) and prefire adults (gray boxes) of black spruce (*Picea mariana*) and white spruce (*Picea glauca*) across the edaphic gradient from left (cold/wet; typical black spruce habitat) to right (warm/dry; typical white spruce habitat) along the sequence of site types Moss, *Ledum*, *Equisetum*, and Slope. Boxes indicate the interquartile range, whiskers indicate the extremes (excluding outliers), and horizontal lines indicate the outliers (>1.5 interquartile lengths from the median).

individuals/m²), intermediate in the *Equisetum* site type, and low (<0.2 individuals/m²) in the Slope site type before the fire. Thus, the Moss and *Ledum* site types represent typical adult black spruce habitats, while the *Equisetum* and Slope site types represent typical adult white spruce habitats.

Postfire recruitment patterns were similar to prefire adult distributions for black spruce but not for white spruce. Postfire black spruce density was highest on the Moss and *Ledum* site types (Fig. 4). In contrast, white spruce regeneration did not exhibit a clear association with site type (Fig. 4), even though *Equisetum* and Slope types (typical adult white spruce habitats) were sampled close to the unburned forest edge where white spruce seed rain should be relatively high (Fig. 3H).

In the best candidate model for black spruce recruitment, posterior parameter means imply a global

(i.e., background) seed rain of 110 seeds/m², plus an additional 50 seeds/m² per m² of prefire black spruce basal area (Table 2). Across all plots, the mean prefire black spruce basal area was 6.9 m²/ha (range 0–41.7 m²/ha), so the mean estimated black spruce seed rain is 454 seeds/m². Seedling establishment was negatively related to DCA1, postfire organic layer thickness *olt*₀, and DCA2 in decreasing order of influence (Table 2). The highest establishment rates and recruitment densities were both found at low values of *alto* and DCA1 (Fig. 5).

In the best candidate model for white spruce recruitment, predicted seed rain at distances of 100, 300, and 800 m from the source stand was 55.1% (95% credible interval [CRI], 28.6–83.8%), 15.2% (6.8–31.2%), and 2.9% (1.2–5.8%), respectively, of the seed rain at 0 m. The response of white spruce establishment to *olt*₀ depended upon the edaphic conditions. Under warm, dry conditions (positive values of DCA1), white spruce establishment rate decreased with *alto*, as was the case with black spruce. In contrast, under cool, moist conditions (DCA1 scores < -1), white spruce establishment rate increased with *alto* (Fig. 5). White spruce establishment rates were highest in the Moss site type, where black spruce, not white spruce, was the dominant prefire species (Fig. 5B, D). White spruce establishment rate decreased with grass cover (Table 2).

There was a significant difference in mean black spruce height between the Moss and the *Ledum* site types (47.3 and 36.4 cm, respectively), but no systematic differences between typical black spruce sites (Moss, *Ledum*) and typical white spruce sites (*Equisetum*, 51.5 cm; Slope, 39.2 cm; Fig. 6). In contrast, the mean recruit height of white spruce was significantly lower in the Moss and the *Ledum* site types (27.0 and 26.1 cm, respectively) than in the *Equisetum* and Slope site types (47.8 and 42.9 cm, respectively). Mean white spruce height was significantly shorter than black spruce in the Moss and *Ledum* sites. Mean recruit height was not significantly different between the two species on the *Equisetum* and Slope site types.

Within all site types (Moss, *Ledum*, and combined *Equisetum*/Slope) mean recruit age *A* at a given height was broadly similar for the two species, and the posterior credible intervals overlapped over most of the height range (Fig. 7). Small but significant differences in *A* occurred at recruit heights 65–140 cm on the Moss site type and 45–120 cm on the *Equisetum*/Slope site type, with white spruce growing slightly faster (smaller *A*) in both cases. While differences between the two species were not pronounced, there were clear differences between site types. Recruits of both species grew faster on the *Equisetum*/Slope than on the Moss site type. On the Moss site type it took black spruce and white spruce recruits 18.2 yr (95% credible interval [CRI], 17.6–18.8 yr) and 16.9 yr (16.0–17.9 yr), respectively, to reach a height of 100 cm, whereas on the *Equisetum*/Slope site type it took them

TABLE 2. Posterior means and credible intervals (CRI) for parameters in the best candidate models of white and black spruce recruitment.

Parameter	Variable	Mean	CRI 0.025	CRI 0.975
Black spruce				
β_0	intercept	-6.043	-7.21	-4.18
β_1	olt_0	-0.397	-0.738	-0.053
β_3	DCA1	-1.261	-1.622	-0.913
β_4	DCA2	-0.371	-0.696	-0.0113
b_1	source intercept (global seed rain)	110.1	17.4	247.6
b_2	prefire basal area (local seed rain)	49.9	3.51	154.4
r	negative binomial shape parameter	0.693	0.496	0.935
White spruce				
β_0	intercept	-4.959	-5.397	-4.465
β_1	olt_0	-0.502	-0.783	-0.215
β_2	g	-0.361	-0.705	-0.0211
β_3	DCA1	-0.753	-1.087	-0.424
β_4	DCA1 $\times$ olt_0	-0.618	-0.927	-0.316
w_1	source strength (seed rain at 0 m)	208.0	192.2	224.0
w_2	shape2	21630	1661	86650
w_3	shape1	0.955	0.572	1.787
r	negative binomial shape parameter	1.344	0.943	1.845

Note: See Methods: Establishment predictor variables and Statistical modeling of recruitment functions for explanations of variable abbreviations.

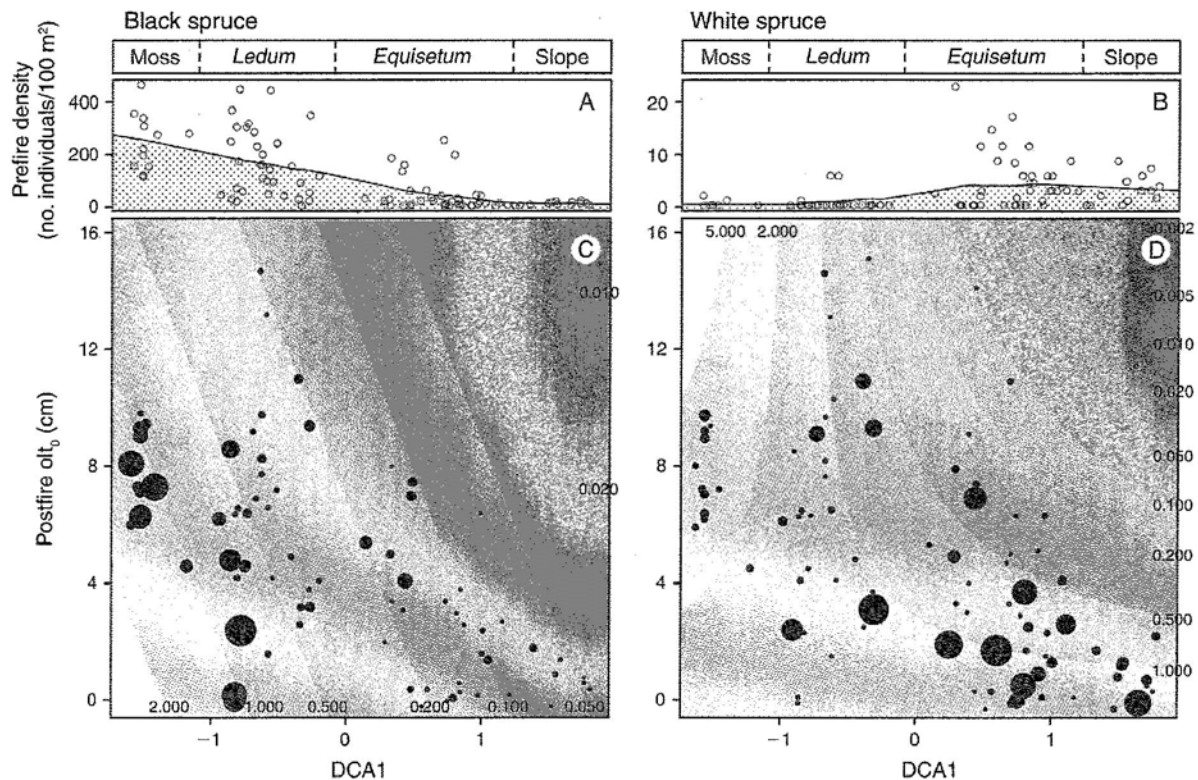


FIG. 5. Prefire adult densities and postfire establishment rates and recruit densities for (A, C) black spruce and (B, D) white spruce along environmental gradients. Soil moisture decreases with detrended correspondence analysis axis 1 (DCA1; x-axis), and burn severity decreases with residual postfire organic layer thickness, olt_0 (y-axis in panels C and D). Curves in panels (A) and (B) were fit as in Fig. 3. Shading and contour lines in panels (C) and (D) show variation in establishment rates (percentage of arriving viable seeds that survived to 21 years postfire). Establishment rates were estimated using the posterior mean parameter values from the recruitment models (Table 2). Sample plots with ≥ 1 recruits are shown as points with the radius proportional to the observed recruit density (black spruce range, 2–838 individuals/100 m²; white spruce range, 2–375 individuals/100 m²).

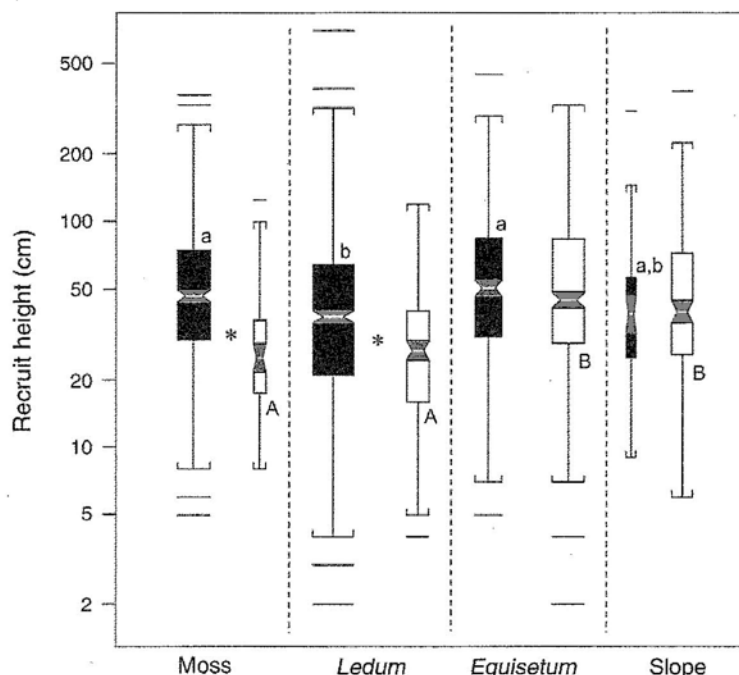


FIG. 6. Median heights (note log scale) of black spruce (black boxes) and white spruce (white boxes) within the four site types (separated by vertical dashed lines). Boxes indicate the interquartile range, notches indicate the approximate 95% confidence interval of the median, whiskers indicate the extremes (excluding outliers), and horizontal lines indicate the outliers (>1.5 interquartile lengths from the median). The width of boxes is proportional to the square root of the sample size. Significant differences ($P < 0.05$) between species within site types are indicated by an asterisk (*). Letters indicate groups within species across site types that were not significantly different (Tukey's method with significance level $\alpha = 0.05$).

only 15.8 yr (15.0–16.7 yr) and 14.8 yr (14.3–15.3 yr), respectively. Growth on the *Ledum* site type was intermediate.

Far (≥ 300 m) from the unburned forest edge, the median estimated white spruce recruit age was 12.3 yr (95% CRI, 11.1–13.3 yr). The estimated age distribution of black spruce in the “far” region was left skewed and significantly older (median, 14.9 yr; 14.4–15.4 yr) than

that of white spruce. The first mast year for white spruce occurred four years after the fire (black arrow at far right in Fig. 8), whereas the seeds of the semiserotinous black spruce were available immediately after the fire. The age difference was less pronounced in the near region (<300 m from forest edge), but still significant (white spruce, 13.2 yr [95% CRI, 12.6–2.8 yr]; black spruce, 14.3 yr [13.7–14.9 yr]).

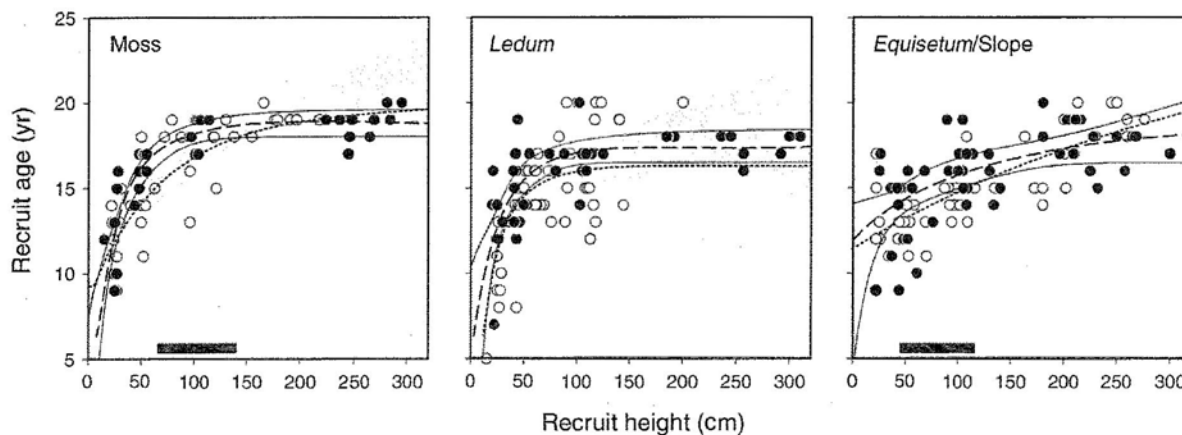


FIG. 7. Recruit age vs. height for white spruce (open circles) and black spruce (solid circles) for three site types (Moss, *Ledum*, and combined *Equisetum*/Slope). Mean predictions and their 95% posterior credible intervals are indicated by a dashed line and solid lines, respectively, for black spruce and by a dotted line and a gray area for white spruce. Horizontal black bars at the bottom of the graph indicate the height range over which the age–height curves are significantly different (see Appendix G).

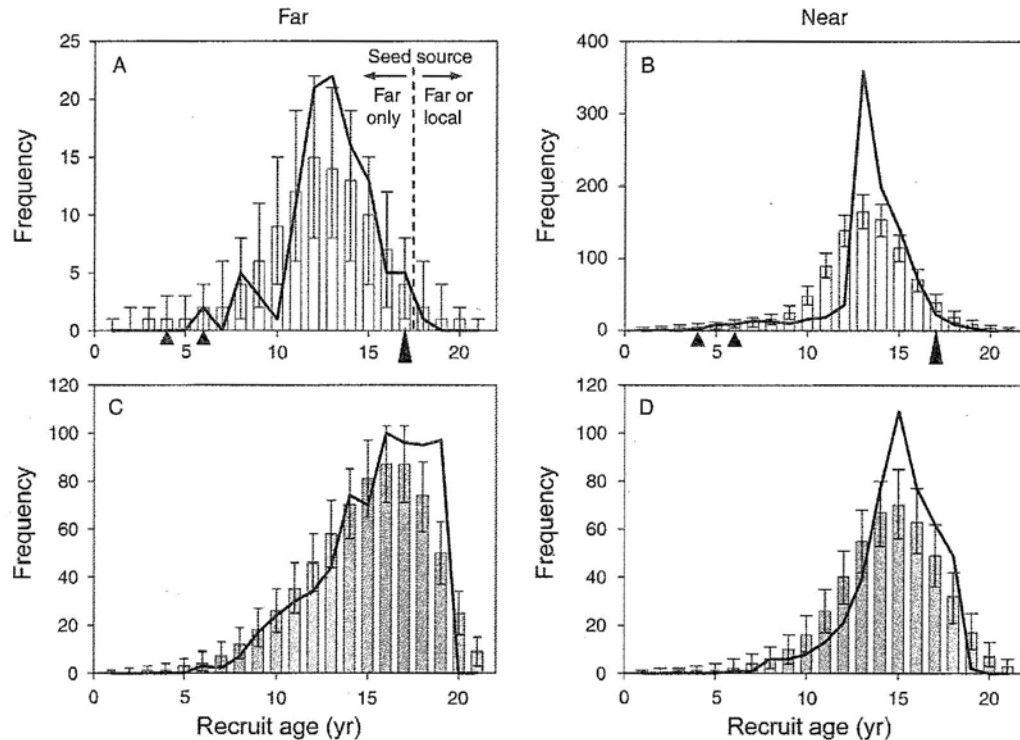


FIG. 8. Age-distributions of recruits of (A, B) white spruce and (C, D) black spruce <300 m ("near") and ≥ 300 m from the unburned forest edge ("far") 21 years after the Rosie Creek fire in 1983. Histograms were obtained by converting height distributions of recruits in plots into age distributions using the age–height functions in Fig. 7. Histogram bar heights and 95% prediction limits (error bars) were obtained from propagating uncertainty in individual recruit ages predicted from measured heights. Lines show the results of the direct conversion without error propagation. Black arrows indicate mast years of white spruce, with arrow size indicating the density of seed production. The vertical dashed line in panel (A) for white spruce in the "far" region separates recruit ages with different potential seed sources (see *Discussion*).

DISCUSSION

We studied dispersal, establishment, and juvenile growth of white and black spruce in a regenerating burn that extends from dry, upland soils (typical habitat of white spruce adults) to moist, mossy, floodplain sites over permafrost (typical habitat of black spruce adults). Our main results can be summarized as follows: On typical black spruce habitat >700 m from the nearest white spruce seed source, the density of white spruce recruits was sufficient to form a fully stocked stand. Recruitment densities this high were unexpected for white spruce hundreds of meters from its seed source because seed trap studies (see *Long-distance dispersal*, below) suggest that white spruce seeds rarely disperse this far and because these areas of the burn were dominated by black spruce before the fire. Our analysis suggests that white spruce was able to form a sapling bank far outside of its adult range for two reasons: (1) Long-distance dispersal events, possibly via secondary dispersal over snow, appear to be more common for white spruce than previously thought. (2) Establishment rates of white spruce were highest in the "alien" floodplain black spruce habitat. Across all site types, height growth rates were similar for recruits of both species, but on typical black spruce sites far from the unburned forest edge, white spruce was younger (and,

therefore, shorter) than black spruce. This age and size difference is likely due to the four-year lag between the fire and the first postfire white spruce mast year (Fig. 8). Black spruce recruits were found primarily in moist areas of the burn that were dominated by black spruce before the fire. This was expected from previous work showing that most black spruce seeds disperse locally (Greene et al. 2004) and from the well-known association of black spruce with moist edaphic conditions (Viereck et al. 1993). In summary, white spruce recruits reached high density outside of their typical adult habitat, whereas black spruce recruits were found primarily within their adult habitat. In our study area there was no indication that dispersal, establishment, or edaphic constraints on juvenile growth limit white spruce's capacity to invade typical black spruce stands during the recruitment stage. We now discuss the validity of these findings and their relation to previous studies.

Long-distance dispersal

Our model of white spruce seed rain, which was fit to data on recruit densities, suggests longer dispersal distances than studies of spruce dispersal based on seed trap data (Fig. 9A; Squillace 1954, Crossley 1955, Ronco 1970, Randall 1974, Dobbs 1976, Zasada 1986, Rupp

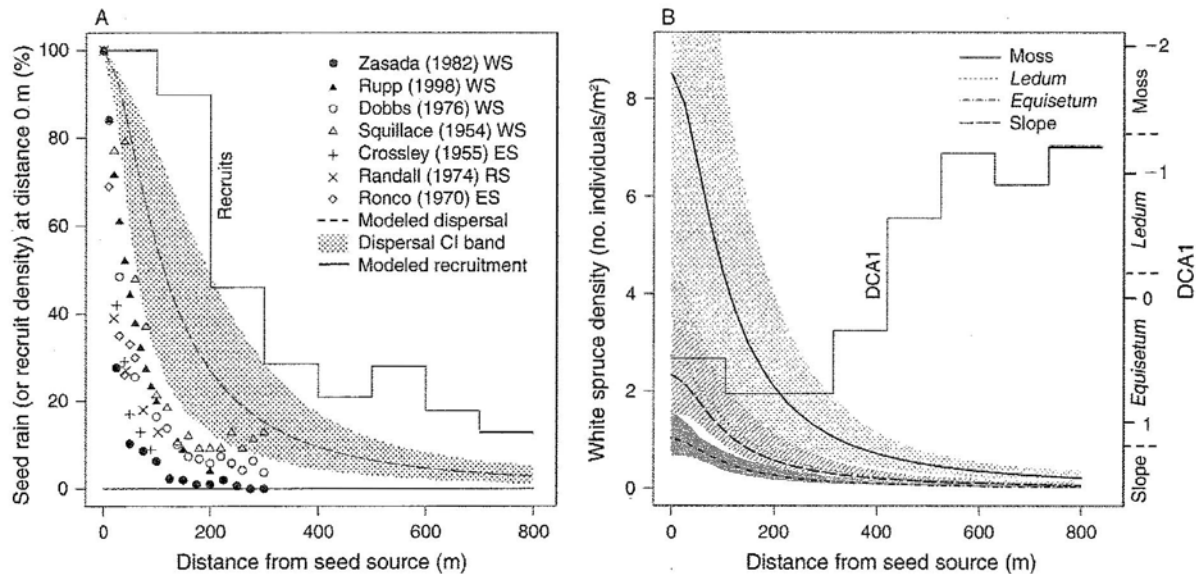


FIG. 9. Comparison of measured seed shadows, our modeled seed rain function, and different recruitment shadows. (A) Seed shadows of spruce forest edges, expressed as the percentage of seed rain at 0 m from the edge, estimated from our model (the shaded area is the 95% posterior credible interval [CRI]) and from seven seed trap studies. Seed rain from all studies is assumed to be 100% at 0 m (not all symbols are visible at 0 m due to overlap). Our study was conducted several kilometers from those of Zasada (1986) and Rupp (1998; Fig. 1B). The maximum distance in the seed trap studies was 300 m. The 95% CRI for our modeled seed shadow excludes the seed trap data at all distances except for the data from Squillace (1954), whose traps were positioned on a steep north-facing slope with wind from the south. The step function shows predicted recruitment density (expressed as the percentage of density at 0 m) in 100-m bands. Predicted recruitment density was calculated as predicted seed rain $\times$ predicted establishment probability using the posterior mean parameter estimates and the mean values of each establishment predictor in each 100-m band. Abbreviations following references are: WS, white spruce; ES, Engelmann spruce; RS, red spruce. (B) Recruitment functions and 95% CRIs for the four site types. The 95% CRI for the Slope type is not shown because it is nearly the same as that of the *Ledum* type. Highest recruitment densities are predicted for the Moss site type (typical black spruce habitat) and lowest for the *Equisetum* type (typical white spruce adult habitat). Mean values of detrended correspondence analysis axis 1 (DCA1) in 100-m bands show that edaphic conditions progress from dry to moist with increasing distance from the seed source in our study area, which explains the divergence of the seed rain and recruitment functions in panel (A). Means and credible intervals for the seed rain curve in panel (A) and the density curves in panel (B) were generated by monitoring a posterior distribution for each relevant quantity at 25-m intervals from 0 to 800 m.

1998, including data from *Picea engelmannii* and *Picea rubens*). Interpolating the data from the seven seed trap studies we estimate that seed rain halved at a mean distance of 31 m (range 13–57 m). Seed traps, unlike vegetation plots, often sample too small an area to detect rare dispersal events far from the seed source (Nathan and Muller-Landau 2000); thus, seed trap studies rarely report data for distances >300 m, a distance at which Zasada (1986), Dobbs (1976), and Squillace (1954) measured 0%, 3.7%, and 12.9%, respectively, of the seed rain at the forest edge (i.e., at 0 m). In contrast, our model predicts 15.2% (6.8–31.2% [95% CRI]) at 300 m and still 2.9% (1.2–5.8% CRI) at 800 m. Interestingly, the high values from the Squillace (1954) study reaching into the credible interval of the modeled dispersal function were obtained from an exceptionally steep north-facing transect (30° – 50° slope vs. $16^{\circ} \pm 11^{\circ}$ for our Slope plots) with the main wind direction from the south.

Long-distance dispersal has been related to wind updrafts (Horn et al. 2001) and to secondary dispersal (e.g., by seed movement over snow during winter;

Greene et al. 1999). Secondary dispersal may be especially relevant for white spruce because $\sim 30\%$ of the seeds abscise on snow (Dobbs 1976, Greene et al. 1999; but see Greene and Johnson 1997). The especially fat recruitment tail we observed along the southern transects (Fig. 3B) could be influenced by several factors: (1) The seed source was elevated 80 m above the floodplain, as opposed to a maximum drop in elevation of 15 m along the northern transects. Mechanistic models suggest that dispersal distance is sensitive to the release height of seeds (Greene and Johnson 1996). (2) Two of the three northern transects were oriented against the mean wind direction (68°), whereas all southern transects were oriented perpendicular to the wind. However, the effects of elevation and wind direction cannot explain the discrepancy between our results and the seed trap data of Zasada (1986) and Rupp (1998), which were collected from a nearby site with similar topography and wind patterns (Fig. 1B). (3) Finally, scattered prefire white spruce adults in the burn may have released viable seeds that somehow survived the fire (Archibald 1980). If so, some seeds could have

dispersed locally into the areas that are now far from the forest edge. Assuming that severely damaged trees are not healthy enough to initiate a new cone crop and given that white spruce seeds remain viable for a maximum of two years (Wagg 1964, Nienstaedt and Zasada 1990), recruits originating from such seeds could not have been younger than 18 yr old at the time of sampling (2004; 21 years postfire) if we allow for an additional year of cone ripening on the dying mother tree. Our data on the age of recruits (Fig. 8), which were collected in the tail of the seed rain function (300-750 m from the seed source), show that 94.1% (95% CRI = 90.1–97.8%) of white spruce recruits were younger than 18 yr. This suggests that even at the farthest distances from the source stand that we studied, >90% of the white spruce recruits originated from seeds that dispersed into the burn from the unburned forest, as opposed to local dispersal from prefire adults within the burn.

Substrate and establishment

Previous studies have shown that seedling establishment rates of white and black spruce vary strongly with substrate (Eis 1967, Zasada 1971, Purdy et al. 2002, Greene et al. 2004, Johnstone and Chapin 2006a). For both species, the percentage of seeds that establish tend to be higher on mineral soil (0.8% and 18% for white and black spruce, respectively, based on the papers cited above) than on organic substrate (0.1% and 3.2%). Although our data do not allow for strong inferences on absolute levels of seed rain and seedling survivorship (Appendix B), our estimated establishment rates for both species (0.05–3%) are similar to estimates from other studies. Previous studies of white spruce establishment have been restricted to upland sites. In contrast, our study included both upland and floodplain sites, and our results suggest that both species had higher establishment rates in the floodplain. Specifically, our analysis suggests that for both species, establishment rates were highest in mossy wet depressions with a thick residual postfire organic layer ($olt_0 \sim 10$ cm). In contrast, Johnstone and Chapin (2006a) reported low spruce establishment rates if olt_0 exceeded 2.5 cm. We believe this discrepancy is due to the moister site conditions in our study than those sampled by Johnstone and Chapin (2006a). Indeed, in our study, black spruce establishment rates decreased with olt_0 , but this was more than compensated for in mossy depressions by the increase in establishment with soil moisture (DCA1). Similarly, in our study, white spruce establishment rates decreased with olt_0 on dry upland sites, which is consistent with previous studies, but increased with olt_0 on moist floodplain sites. These results suggest that organic substrate provides favorable establishment conditions for both species if the site is sufficiently moist, but that organic substrate does not favor establishment on dry upland sites where organic material is prone to desiccation. This conclusion is supported by Greene et al. (2004), who identified

unburned sphagnum patches on upland sites as good seedbed for black spruce.

Substrate-distance interactions and recruitment in the far end

Along the southern transects, the quality of the seedbed apparently increased with distance from the seed source in the following sequence (Fig. 3F, H): (1) At a distance of 0–100 m, patches of low fire severity resulted in a thick postfire organic layer, which negatively affects establishment success on dry upland sites; (2) from 100–300 m, severe upslope fire resulted in a thin postfire organic layer, which favors establishment on upland sites; (3) beyond 300 m, the edaphic conditions became increasingly wet, leading to high establishment rates for both species, despite the negative effect of the thick postfire organic layer on black spruce establishment. As a consequence, our white spruce recruitment function had a fatter tail than our estimated seed rain function (Fig. 9A), because the decrease in seed rain toward the far end of the transects was partially compensated for by an increase in establishment rate. A similar argument was made for the sequence 1 to 2 by Greene et al. (2005). The impact of substrate moisture on establishment success in our study is illustrated by comparison with recruitment data from an upland site in Quebec, where Galipeau et al. (1997) found postfire white spruce recruits at 1200 m into a burn, but at far lower density (0.08 recruits/m²) than in our study (0.4 recruits/m² at 725 m).

Growth rates and the fate of white spruce recruits under current conditions

Differences between species in height growth rates on different site types were small (Fig. 7) and are unlikely to account for the observation that white spruce recruits were on average 10–20 cm shorter in the *Ledum* and Moss site types, respectively. This observed height difference is most likely due to the younger age distribution of white spruce far (>300 m) from the unburned forest, where the Moss and *Ledum* site types are the dominant habitat (Fig. 2). In this "far" region, we found that white spruce recruits were on average 2.6 yr younger than black spruce recruits (12.3 vs. 14.9 yr). The reason for the age difference is straightforward. While black spruce, a semiserotinous species, could disperse seeds into the burn immediately after the fire, a white spruce mast year did not occur until four years after the fire (right-most black upward arrow in Fig. 8). Peters et al. (2005) studied the interaction between fire history and masting cycles and concluded that white spruce regeneration may be substantially reduced if the mast year is between one and three years delayed in relation to the fire event. This suggests that in our study area white spruce invasion into the floodplain habitat might have been far more intense if fire and mast year had coincided. In the near region (0–300 m from the forest edge) the age difference between white and black



PLATE 1. White spruce sapling established in a typical black spruce habitat ~600 m away from the upland seed source. The discoloration of the needles indicates a beginning nutrient limitation not yet reflected, however, by declining growth rates. The charred stems are black spruce snags left over from the Rosie Creek fire in 1983. Photo credit: C. Wirth.

spruce was only 1.1 yr and was not significant. This smaller age difference was probably due to the fact that close to the forest edge a larger fraction of the population originated from background seed production between the last years. In summary, our results suggest that differences in growth rates of recruits were small on all site types and that height differences were due to age differences, which, in turn, were due to differences in the timing of seed dispersal.

White spruce expansion: the role of edaphic factors

In our study area there was no indication that dispersal, establishment, or edaphic constraints on juvenile growth limit the capacity of white spruce to invade typical black spruce stands during the first 21 years of postfire regeneration. In contrast, prefire adult populations of black and white spruce were clearly separated across the edaphic gradient we studied (Figs. 4 and 5A, B), and it is known that white spruce is less well adapted to permafrost soils than black spruce (Chapin 1986, Van Cleve et al. 1991). Hence, we suspect that under an unaltered climate, most white spruce recruits in the floodplain would not persist to the adult stage if the permafrost returned to prefire levels as a consequence of

the development of an insulating moss layer during postfire succession. Although mean growth rates over the 21-year postfire period were similar for the two species, needle discoloration (see Plate 1) and reduced needle nitrogen and potassium concentrations in floodplain white spruce (but not black spruce) suggest that white spruce recruits in the floodplain are already beginning to suffer from nutrient limitation (C. Wirth, *unpublished data*). However, an anticipated degradation of permafrost associated with continued climate warming may improve growing conditions for white spruce. Depending on topography, substrate, and precipitation regime, permafrost degradation may lead to site deterioration through water-logging or to site improvement through soil drying and warming (Jorgenson and Osterkamp 2005 and citations therein). The latter would favor white spruce and may allow this species to persist on or even take over sites currently dominated by black spruce. A recent remote-sensing study has documented pond shrinking throughout the interior of Alaska (Riordan et al. 2006). This landscape-level "drying" has been related to permafrost degradation associated with improved drainage and/or increased evapotranspiration. In both cases soil hydrological and soil thermal conditions are expected to change in favor of white over black spruce. In both the upland and floodplain areas of the Rosie Creek burn there exists a dense network of drainage channels, so that surplus water from permafrost melting may be discharged rapidly toward the Tanana River, thus favoring a transition to a more white spruce-dominated landscape.

White spruce expansion: landscape-level interaction of dispersal and fire regime

Many vegetation models addressing the response of vegetation to climate change assume global availability of recruits and thus ignore the processes of dispersal and establishment. This is the case for most climate envelope models of equilibrium vegetation distribution (Prentice et al. 1992, Tchebakova et al. 1993) and also for many coarse-resolution dynamic global vegetation models (e.g., Sitch et al. 2003). In both model types, vegetation responds instantaneously to changes in the environment. In contrast, more sophisticated regional vegetation models predict a delay in climate-driven vegetation transitions due to dispersal limitation (Scheller and Mladenoff 2005). Our results show that white spruce formed a persistent sapling bank in distant floodplain areas, probably due both to long-distance dispersal and high establishment rates on moist, organic substrates. This suggests that advance of white spruce into burned black spruce habitats may not be delayed by dispersal limitation; i.e., the assumption of global availability of recruits may be valid, assuming that all areas of the burn are within some maximum distance of a white spruce seed source. Our results suggest that this maximum distance is at least 700 m. Eberhart and Woodard (1987) analyzed fires in Alberta and quantified the fraction of burned area

within a certain distance of residual stands (i.e., potential seed sources). They show that even in their largest fire size class (2000-20000 ha) 86% of the burned area was within 500 m of a residual stand. This percentage may also be representative for the interior of Alaska where ~80% of the burned area is in fires larger than 4000 ha (DeWilde and Chapin 2006). Although exact numbers are lacking, the likelihood that white spruce is present in residual stands is probably high. This is because white spruce and black spruce occur in a fine-grained landscape mosaic across much of the interior of Alaska and transitions between the two habitats are often gradual and interpenetrating. On upland sites, white and black spruce occur on adjacent south- and north-facing slopes, respectively, and in floodplains dominated by black spruce, white spruce is common in gallery forests along river channels (Viereck et al. 1993). In addition white spruce tends to burn less frequently than black spruce forests (Cumming 2001, Wirth 2005) and is thus likely to represent a larger fraction of the residual stands. The above observations imply that in the great majority of burns in the interior of Alaska white spruce regeneration should not be dispersal-limited and dense regeneration may be widespread. This hypothesis is easily tested in the field using the new method we have presented for identifying spruce recruits (Appendix A).

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APPENDIX A

Field identification of spruce recruits based on needle anatomy (*Ecological Archives* M078-019-A1).

APPENDIX B

Logistic regression model to predict species identity of dead spruce based on morphology (*Ecological Archives* M078-019-A2).

APPENDIX C

Derivation of a Bayesian prior for white spruce seed rain at distance zero from the seed source using seed trap data (*Ecological Archives* M078-019-A3).

APPENDIX D

Implications of wind speed and direction for white spruce seed dispersal (*Ecological Archives* M078-019-A4).

APPENDIX E

Derivation of negative binomial distribution for the number of recruits (*Ecological Archives* M078-019-A5).

APPENDIX F

Cover of selected understory species in the four site types and additional comments on the vegetation survey (*Ecological Archives* M078-019-A6).

APPENDIX G

Age-height functions: model fitting procedure and error propagation (*Ecological Archives* M078-019-A7).

APPENDIX H

Ranges and means of dependent and predictor variables for site types and all plots combined (*Ecological Archives* M078-019-A8).